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The Shoot Apex in Angiosperms .. Ernest M. Gifford, Jr. 477

FUTURE CONTENTS
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THE BOTANICAL REVIEW

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THE SHOOT APEX IN ANGIOSPERMS

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Introduction 477
Gymnosperms 478
Angiosperms 479
Topographical aspects 479
Tunica-corpus concept 479
Mantle-core concept 481
Histogenic-layers concept 482
"L'anneau initial" concept 484
"Méristème d'attente" concept 486
Concepts of inflorescence and floral meristems 491
Cytohistological aspects 492
Occurrence of zonation 492
Differentiation and dedifferentiation 496
Variability in size and structure 497
Growth–size correlations 497
Plastochron variations 498
Seasonal variations 502
Variations in relation to age of the plant 502
Effects of treatments other than those with colchicine 508
Typology 509
Phylogeny 511
Conclusions 515
Acknowledgments 517
References 523

INTRODUCTION

An encouraging amount of information has been accumulated during the past two decades relative to the structure and growth of the shoot apex in vascular plants. Nevertheless, the total number of investigated forms, particularly in the angiosperms, is insignificant when compared with the total number of extant species or even genera. As an example, a descriptive enquiry into apical structure of a series of closely related angiosperm species might serve as a guide from which general conclusions could be made concerning the course of future studies into the structure and growth of this formative region of the plant. If recognizable differences and exceptions exist in the structural aspects of the

shoot apex, either they can be dismissed as unimportant or they can serve as a stimulus for further investigation. The enquiring mind accepts the latter view and demands more carefully recorded observations. Unfortunately, descriptive limits are not easily reached when intensive and extensive studies are undertaken of single characters. Furthermore, complete information is essential and mandatory if answers of a causative nature are sought through experimental treatment and manipulations.

There are several comprehensive reviews of the various interpretations of the structure and activity of the shoot apices in vascular plants (Foster, 1939*b*, 1941*a*; Sifton, 1944; Philipson, 1949; Johnson, 1951; Popham, 1951; Esau, 1953). In the present paper an attempt will be made to review critically the more recent literature pertaining to the shoot apices of seed plants, particularly the angiosperms.

Gymnosperms

In the shoot apices of the majority of gymnosperms all primary tissues can be traced ultimately back to a group of apical initials which divide anticlinally and periclinally (Fig. 1). The following genera exemplify this mode of growth: *Ginkgo* (Foster, 1938),

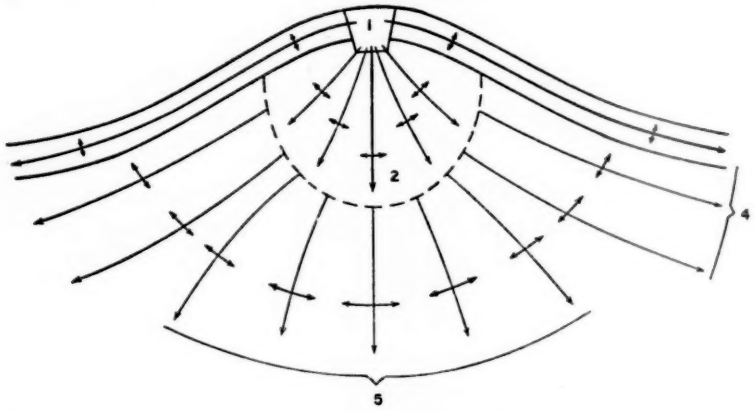

Fig. 1. Diagrammatic representation of the zonation and direction of growth in the shoot apex of *Ginkgo biloba*. *Zone 1*—apical initial group, the ultimate site of origin of all subjacent tissues; *Zone 2*—central-mother-cell zone, a cup-shaped mass of large, slowly dividing cells; *Zone 3*—represented by the broken outline, which is to indicate a transition in growth from that of *Zone 2* to the actively dividing cells of the lateral and basal regions; *Zone 4*—peripheral zone; *Zone 5*—rib meristem (after Foster).

Cycas (Foster, 1939*a*, 1940), *Dioon* (Foster, 1941*b*), *Microcycas* (Foster, 1943), *Zamia* (Johnson, 1939), *Torreya* (Kemp, 1943); *Pinus, Picea, Abies* (Korody, 1937), *Sequoia* (Sterling, 1945), *Pseudotsuga* (Sterling, 1946). In certain gymnosperms a more or less discrete outer layer is present, with a group of initials located beneath this layer dividing in various planes. Examples of such structure are found in certain genera of the Taxodiaceae, among members of the Gnetales (*Ephedra*, Gifford, 1943; *Gnetum*, Johnson, 1950, 1951) and in the genus *Araucaria* (Griffith, 1952). In addition to the growth zones, the apices of many gymnosperms show variable cytological zonation patterns (for reviews, see Foster, 1949, and Johnson, 1951). Foster (1949, p. 32) has suggested that perhaps the more definitely stratified cell arrangement represents the more advanced type of apical structure. This suggestion is worthy of serious consideration in connection with surveys of apical structure in vascular plants; reference to this point will be made later.

Angiosperms

Topographical aspects

TUNICA-CORPUS CONCEPT. In angiosperms the shoot apex can be described in terms of planes of divisions of a cell or of groups of cells. The tunica-corpus concept (Schmidt, 1924) has long been a useful tool in the description of the shoot apex of angiosperms. The tunica consists of a layer or layers of cells in which divisions are predominately anticlinal. The corpus represents another initiation zone in which cell divisions occur in various planes (Fig. 2).

The tunica and corpus are considered to be two interdependent growth zones; anticlinal divisions in cells of the tunica serve to maintain the proper balance between surface growth and growth in volume of the shoot apex. Also, there is no commitment as to derivatives of the two growth zones. Leaves may have their origin in the tunica or corpus and at maturity may consist entirely of derivatives of the tunica or of combinations of both tunica and corpus derivation. Likewise, the vascular system and cortical tissues vary in their origins from the tunica and corpus initials. The pith is generally derived from the corpus.

As originally defined, the term "tunica" applied to a layer or

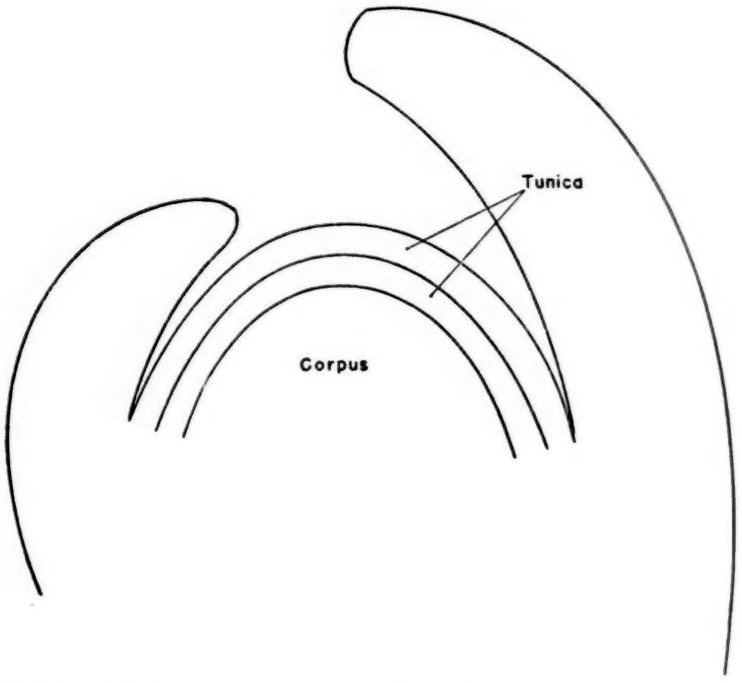

FIG. 2. Diagram depicting the original interpretation of the growth of an angiosperm shoot apex based on the tunica-corpus concept.

layers of cells in the shoot apex in which divisions are anticlinal except where leaf primordia arise. In plants investigated by Schmidt (1924), the number of tunica layers of an established apical meristem remained constant during a plastochron (the interval between the initiation of two successive leaves). The upper corpus cells displayed stratification during the maximal area phase of the shoot apex; periclinal divisions interrupted the continuity of corpus layers during minimal area phase of a plastochron. The tunica and corpus were variable in their contributions to developing leaves and buds, which indicated a definite interdependence of the two growth zones.

Anatomists, disturbed by the rigidity of the Hanstein histogen theory, enthusiastically accepted this new approach toward an understanding of the developmental problems inherent in the study of the shoot apical meristem. When this theory was tested on addi-

tional genera and species, it was found that considerable variation exists as to the stability of the tunica layers above the youngest definable leaf (Foster, 1935; Boke, 1940; Reeve, 1948*a*; Rouffa and Gunckel, 1951; Millington and Gunckel, 1950; Gifford, 1950). Even with these demonstrated fluctuations most workers have continued to utilize the tunica-corpus terminology because of its usefulness in describing growth activities of the apical meristem. Moreover, it removes any connotation of predestination for specific cell lineages.

MANTLE-CORE CONCEPT. The use of a "loosely applied" tunica-corpus terminology has been criticized by Popham and Chan (1950). These workers think that, since the term "tunica" originally applied to a layer or layers which remain discrete because of anticlinal divisions, and since this discreteness is only relative, the tunica-corpus concept should be replaced by a more suitable one. Instead of "tunica" the authors propose using "mantle layers" and define the latter term in such a way as to take into account the observed variations in the number of surface layers, particularly the inner layers, of a given species. If, topographically, one wishes to designate the cells underlying the mantle layers, use of the term "core" is suggested (Popham and Chan, 1950). The term "corpus" is not favored because "the term corpus when used to include such a heterogeneous assemblage of growth zones is likely to convey a confused, oversimplified and erroneous concept of shoot growth, if indeed it conveys any at all" (Popham, 1951).

In the original announcement of the tunica-corpus theory, as mentioned before, the tunica was interpreted as being composed of evident layers of a constant number. Schmidt (1924) considered using the terms "Mantel" and "Kern" (core) for the growth regions of the apical meristem but he hesitated to adopt these terms because Buder (1915) already had utilized "Mantel" and "Kern" in describing the shoot apices of plants identified as periclinal chimeras. In the words of Buder, "Ich will den Anteil der zentralen Komponente als Kern, den der peripheren als Mantel bezeichnen". In this connection, if the apical meristem of a plant is a stable periclinal chimera and involves more than a single outer layer, no periclinal divisions should occur in cell layers comprising the "Mantel". "Mantle" and "core", it would seem, have

established meanings already. Therefore, it would appear that if the points in question are those of priority (based upon an original description), and a desire to convey the interrelationships of growth zones, a flexible use of the terms " tunica " and " corpus " has more merit than the introduction of another set of terms which also must receive qualified usage.

Only by extensive studies can the minimal and maximal limits of stratification be obtained for any given species. The work of Schnabel (1941) is representative of the type of intensive study that should characterize every work on the organization and development of the shoot apex. By a study of all phases of a plastochron in *Silene maritima,* Schnabel found the following:

Number of shoots	Number of tunica layers			
	Definitely 4 layers	Definitely 3 layers	Periclinal divisions in T_3	Periclinal divisions in T_2
128	40.6%	55.5%	2.4%	1.5%

From these results, Schnabel (1941) concluded that *Silene maritima* has a three-layered tunica. The principal activity of the outer three layers is in surface growth, but statistically he shows that periclinal divisions do occur, even in T_2. The frequency of periclinal divisions in T_2 is low but illustrates that the autonomy of the two subsurface layers is not absolute. Similar divisions in the apex of a 2–4–2 plant of cranberry (Dermen, 1947) would establish the more stable form, 2–4–4 (see below). Additional studies by Schnabel (1941) included *Honckenya peploides, Dianthus caryophyllus* and *Clematis paniculata.*

HISTOGENIC-LAYERS CONCEPT. As a result of studies on naturally occurring periclinal cytochimeras in apple and periclinal cytochimeras in cranberry and peach induced by colchicine treatment, Dermen (1947, 1951, 1953) has suggested that tunica-corpus designations in these plants be replaced by reference to " primary histogenic layers ". According to this idea, there are three basic histogenic layers in the plants studied (" and perhaps in all other angiosperms ", Dermen, 1951), and these are designated as L-I, L-II and L-III. Various combinations of ploidy of these layers exist in the shoot apices studied. The cells of L-I (the outermost layer) may be $2x$, those of L-II, $2x$, and those of L-III, $4x$. Expressed differently, the apex would have the constitution, 2–2–4.

Examples of other realized possibilities are 2–2–2, 4–2–2, 2–4–4, 4–4–4 and 2–4–2. Forms having more layers are considered to be derived from the basic types. The least stable form is the 2–4–2 type because a periclinal division in L-II would result in a 2–4–4 type. In stems and leaves the epidermis is derived from L-I. In some stems a 1–3-layered hypodermis or even more cortical tissues may be derived from L-II. In other instances a portion of the vascular tissues may be derived from L-II. In general, vascular tissue and pith have their origin from L-III.

These histological analyses of the cranberry stem indicate that mature primary tissues are in general periclinally arranged, irregularly so in some instances. This arrangement could be anticipated because the apical meristem displays an organization into periclinally disposed layers. The epidermis is derived from the outermost tunica layer. The cortical tissues are derived from the second tunica layer. The second tunica layer and corpus vary in their contributions to the vascular tissue and pith.

On the contrary, Dermen (1947) considers that "the terms 'tunica' and 'corpus' do not have fixed values and fall short of having real meaning, histogenetically or ontogenetically". He further states that "it would be less confusing if these theories and terminologies were put aside and reference were made to tissues merely by their names, such as epidermis, hypodermis, cortex, etc., and reference made, if need be, to apical layers by number, such as L-I, L-II, etc.". These ideas are in a sense a modified version of the Hanstein histogen theory without the implication of absolute tissue predestination. As mentioned later by Dermen (1953), the term "histogenic layer" is perhaps more appropriately applied in a "restricted" sense to known induced cytochimerical plants where derived primary tissues can be subjected to karyological studies.

In an earlier work (Satina, Blakeslee and Avery, 1940), induced periclinal cytochimeras in the shoot apices of *Datura* revealed that three layers of the apical meristem respond independently to colchicine treatment. In cases where there is a difference in chromosomal number between the second and third layers, it was shown that the outer two layers are maintained as discrete strata above the level of definable leaf primordia. It was demonstrated that the outer two layers (tunica) and the third layer

(corpus initials) mutually contribute cells to new organs (Satina and Blakeslee, 1941, 1943). The authors agree that the apices of *Datura* (both vegetative and floral) could be interpreted in terms of the tunica-corpus concept but prefer the term "germ layers".

"L'ANNEAU INITIAL" CONCEPT. According to Plantefol (1947, 1951) and his associates (Astruc, 1949; Bersillon, 1951; Buvat, 1951*d*, 1952), the phyllotaxis of most plants can be expressed in terms of a few (2 or 3) helices. For each foliar helix there are

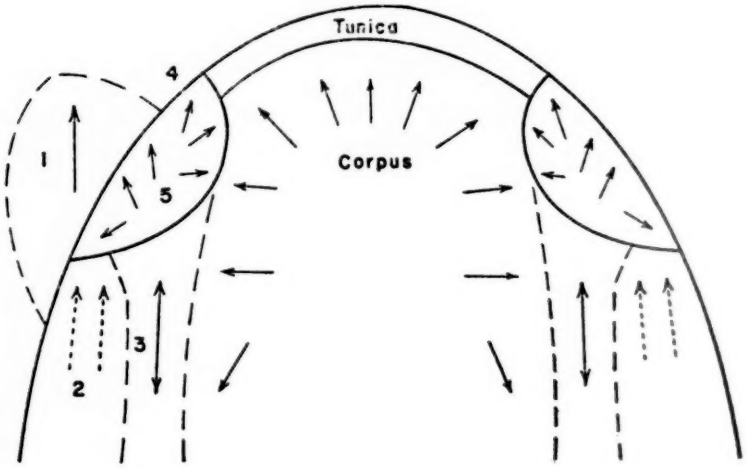

FIG. 3. Diagrammatic representation of a dicotyledonous shoot apex based on the concept of an active foliar initiating ring ("l'anneau initial"). *1*—a leaf primordium ("initium") formed by the "anneau initial"; *2*—parenchymatization of cells on the lower border of the anneau which ultimately delimits the epidermis from the future cortex; *3*—elongating cells, derived from the anneau, which collectively constitute the cylinder—"anneau prodesmogénique"; *4*—reconstitution of the "anneau initial"; *5*—"l'anneau initial". Arrows in the central portion of the shoot apex indicate the main direction of growth of the corpus at successive levels (after Plantefol).

a generative center and an organizer which harmonizes the functioning of the different centers. These workers recognize at the apex an organization that includes tunica and corpus, but their interpretation of the growth of the apical meristem is entirely revolutionary (Fig. 3). A portion of the corpus is the only part of the apex which undergoes any growth of importance. Buvat (1951*d*) speaks of the "méristème médullaire", constituting the lower part of the corpus, and considers it responsible for growth

in length of the axial portion of the stem. The tunica is stretched over the corpus, submitting passively to extension. This would account for the large size of cells in the tunica near the summit and for the paucity of division figures. The real site of growth is in a peripheral region of the tunica where many cell divisions are taking place. This ring of rapid growth is termed " l'anneau initial " and is said to contain the generative centers for potential leaves. Plantefol recognizes that the outer tunica layer is continuous with the epidermis. Despite this continuity, he considers that there is a self-perpetuating ring of cells (l'anneau initial) some distance from the apex. These cells are in the true sense " classical initial cells "—" Dans l'anneau initial, se trouve localisé un méristème actif qui assume le rôle des cellules initiales classiques, sans que rien permette toutefois d'affirmer la présence des cellules permanentes envisageés sous cette appellation " (Plantefol, 1947, p. 67).

At the moment of leaf initiation most of a localized portion of the " anneau " is raised by periclinal divisions in superficial layers (except the outer one) as well as in deeper layers (Fig. 3). As the leaf primordium increases in width and height, cells along the lower edge of the anneau undergo parenchymatization and procambialization, giving rise to future cortical and vascular tissue. Concomitantly, internodal extension is brought about by these processes in conjunction with the action of the " méristème médullaire " (Fig. 5). At the same time on its upper border, the anneau is reconstituted; hence this would assure a nearly constant height for this meristem and provide initials for the next primordium in the same helix.

In a further extension of the theory, Bersillon (1951) states that each sector (the terminus of each helix) of the anneau is in a different developmental phase at any particular moment (Fig. 4). In a transverse sectional view of the anneau three phases can be recognized: (*a*) the " phase morphogène "—active leaf initiation, (*b*) " phase de régénération "—reconstitution of the anneau for leaf initiation later, (*c*) " phase de repose relatif "—resting condition prior to leaf initiation. In the example (*Papaver somniferum*) cited by Bersillon (1951), phyllotaxis can be resolved into two helices, each showing continuity of leaf primordia. He suggests that there are two centers of initiation, nearly opposite, which

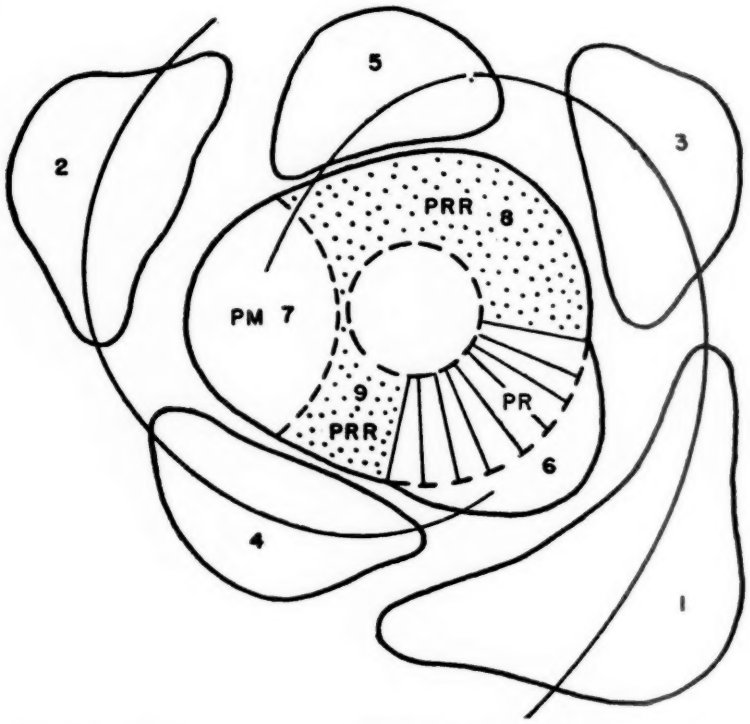

FIG. 4.—Diagram, transverse section of the apical meristem of *Papaver somniferum* at the level of the leaf initiating ring ("l'anneau initial"). Each arc passes through leaves of the same helix. Leaf 7—"l'anneau" in the "phase morphogène", *PM*, (active leaf initiation); Leaf 6—"l'anneau" in the "phase de régénération", *PR*, (reconstitution of the anneau for initiation of next leaf in the helix); potential leaves 8 and 9—"l'anneau" in the "phase de repose relatif", *PRR*, (resting condition prior to leaf initiation) (after Bersillon).

run through the anneau in a regular helical or step-wise manner (Fig. 4).

It is tempting to compare the peripheral portion of the "anneau" of Plantefol with a part of the "cambial-like" zone (Fig. 7) described for certain angiosperms by Popham and Chan (1950) and Popham (1951). According to Buvat (1950*a*, *b*, *c*, see below), the cells of the subapical zone in the apical meristem which exhibit "dedifferentiation" would correspond to those of the "anneau".

"MÉRISTÈME D'ATTENTE" CONCEPT. A new theory of the structure and growth of the shoot apex recently has been proposed by

Buvat (1952). The concept embodies certain ideas of Plantefol (reviewed above). On the basis of cytoplasmic and nuclear studies, Buvat (1952) concludes that the most apical axial-cells of the shoot apices in gymnosperms and in three investigated species of angiosperms (Buvat, 1952, 1953) do not have a histogenic or organogenetic role during vegetative growth. These most apical cells, heretofore considered by most workers as being the center of origin of all subjacent tissues of the primary body, are considered by Buvat to be in a state of inactivity. These cells constitute a so-called " méristème d'attente " during vegetative growth of the plant and are functional only when a terminal flower or inflorescence is formed. Buvat considers that the topographically useful terms " tunica " and " corpus " should be retained but that they do not adequately describe the functional regions of the shoot apex in angiosperms.

According to Buvat, the tunica consists of two parts: (*a*) a central portion (proméristème sporogène) in which mitoses are very rare; (*b*) a peripheral portion, the " anneau initial " (in the sense of Plantefol), in which divisions are numerous. The subsurface layer of the " anneau " provides the initials for leaves.

The corpus (which may have its origin from the second tunica layer during the seedling stage, e.g., *Myosurus*) also is composed of two regions, viz., (*a*) an upper or central portion (proméristème réceptaculaire) with practically no histogenic role during vegetative growth, and (*b*) a lower portion (méristème médullaire), the cells of which function as a rib-meristem giving rise to the pith (Fig. 5).

The ideas conveyed above are presented in outline form below (from Buvat, 1952):

Tunica	Anneau initial Proméristème sporogène	Méristème d'attente
Corpus	Proméristème réceptaculaire Méristème médullaire	

In support of the contention that there is an inactive group of apical cells in the shoot apex, evidence is presented from the plotting of division figures, taken from the superposition of successive serial sections. This method has been applied in studies of *Vicia faba* (Lance, 1952; 1953*a*, *b*), *Lupinus albus* and *Triticum vulgare* (Buvat, 1952, 1953). These workers consider that the results

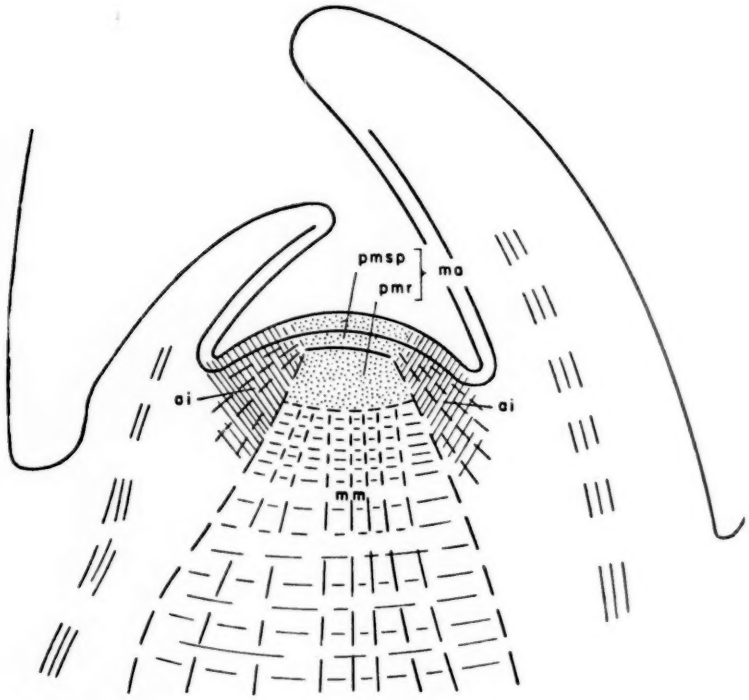

FIG. 5. Diagram, shoot apex of *Cheiranthus cheiri* based on the concept of an inactive apical zone ("méristème d'attente"). *ai*—"anneau initial"; *ma*—"méristème d'attente"; *mm*—"méristème medullaire"; *pmr*—"proméristème réceptaculaire"; *pmsp*—"proméristème sporogène" (after Buvat).

of their studies negate the possibility of the presence of a group of shoot apical initials. Division figures are reported to be concentrated in the "anneau initial" region, thus supporting the general contention held by others (Plantefol, Bersillon, etc.) that the active regions of the axis are essentially lateral and subterminal, not apical.

In spite of the above cited evidence, the idea of a "méristème d'attente" is not supported, in the reviewer's opinion, by the work on periclinal cytochimeras. How is it possible to obtain axial cells of differential ploidy in the surface layer and subsurface layers of buds that possess an organized apical meristem at the time of treatment with colchicine? How is it possible to explain the phenomenon that the cells of an entire tunica layer may be

polyploid if a part of it is inactive? It is questionable that cells in the region of the " anneau ", for example, would respond independently to colchicine and then give rise to derivative cells, arranged in definite strata and occupying a more apical position. This process would require the displacement of an original group of apically disposed cells. Besides, the unstable condition of the so-called " anneau initial " speaks against such a theory. The work of Dermen (1947) also has shown that the stability of a periclinal cytochimera may be only transitory if cells in the most apical position undergo periclinal divisions. The changes that have occurred at the apex are reflected in the altered periclinally arranged tissues at a lower level in the stem (see section HISTOGENIC-LAYERS CONCEPT).

According to Buvat (1952), the existence of an inactive zone in the shoot apex of angiosperms is proved by the absence of mitotic figures. A recent *fait accompli* of cell division is admitted as evidence, for example, in the initiation of leaves in the second tunica layer in *Myosurus* (Buvat, 1952, p. 227, Fig. 13); however, similar cell alignments are not considered by Buvat as evidence for recent cell divisions in the apical initiation zone of shoot apices.

In discussing the results of a study on *Myosurus,* Buvat (1952, p. 241) states that the most apical cells (" Les cellules les plus apicales ") of the vegetative apex do not function as the initials of vegetative organs (" Elles ne sont donc pas initiales d'organes végétatifs "). To most students of the apical meristem these cells have never been thought of as being the initials of organs. The initiation of vegetative organs takes place in cells which have, in turn, been derived from the uppermost or terminal cells of the apical meristem. The four regions of the apical meristem recognized by Buvat correspond in some measure to those described by other workers (see section CYTOHISTOLOGICAL ASPECTS). In the development of any theory of apical organization in seed plants it is most essential to recognize a cytohistological zonation pattern in the apex, superimposed upon a zonal pattern expressed in terms of planes of cell division. And, as Buvat (1952, p. 264) has pointed out, it is extremely important to guard against the establishment of precise limits between zones in the apex (" on distingue quatre territoires, . . . mais entre lesquels il faut se garder d'etablir des limites précises. Chacun d'eux est en effet susceptible de

fournir, par ses bords, de cellules aux territoires voisins"). Recognition of interdependence between growth zones of the shoot apex implies that all cells of the shoot apex are capable of division; however, the frequency of divisions in the various zones may be only relative. Therefore, this labored attempt by Buvat to demonstrate the presence of an inactive zone in the shoot apex is unrealistic despite the evidence furnished up to the present time. Growth of the shoot apex should be considered in terms of its total structure and potentialities.

The concept of a "méristème d'attente" is not restricted by its proponents to angiosperms but is extended to include gymnosperms. Although gymnosperms do not occupy the focal point of interest in this review, a discussion of the structure of the apical meristem in these plants is included because of its relevancy to the general problems associated with studies of the vegetative shoot apex in seed plants.

The interpretation given to the shoot apex of gymnosperms by Buvat (1952) is based upon the studies of Camefort (1950, 1951) on *Ginkgo* and *Picea*. Earlier, Foster (1938, 1939*a*, 1940) had shown that in *Ginkgo* (Fig. 1) and cycads there is a group (variable in number) of apical initials which is the ultimate origin of all cells of the shoot. In all instances the apical initials contribute cells to the central-mother-cell zone, the cells of which enlarge and divide at a reduced rate. Rapid cell division is resumed around the flanks and base of the central-mother-cell zone, resulting in the formation of an active peripheral zone and a basal rib meristem zone. Specifically, it is the above described apical initiation zone and central-mother-cell zone that Buvat (1952) considers as constituting a "méristème d'attente". This idea is not supported for gymnosperms because mitoses have been observed and figured in surface initials and central mother cells of *Ginkgo* (Foster, 1938, Figs. 5 and 8; Plate 26, Fig. 1; Plate 27, Fig. 2). Mitoses have also been described and illustrated for the genus *Cycas* (Foster, 1939*a*, Figs. 3b and 8). Furthermore, the undeniable results of recent divisions are numerous in *Ginkgo, Cycas* and *Microcycas* (Foster, 1943).

The unqualified acceptance of the theory as set forth by Buvat (1952) raises a question relevant to the ultimate function of the most apical cells in certain gymnosperms and certain angiosperms which do not form terminal flowers or inflorescences. If the idea

of Buvat (1952) is correct, it can be concluded only that the cells in question would never function throughout the life of the plant —a questionable conclusion which requires considerably more proof before its unqualified acceptance.

CONCEPTS OF INFLORESCENCE AND FLORAL MERISTEMS. In a well-documented descriptive study of zonal changes that take place in the transformation of a vegetative shoot apex into a reproductive apex, Philipson (1947) has described a gradual change from the zonal pattern characteristic of vegetative apices to that of reproductive apices. In species of *Bellis* and *Succisa* a gradual transition takes place: the peripheral zone of the corpus extends down the flanks of the enlarging apex and the central zone of the corpus is replaced by the peripheral meristem which becomes continuous over the apex. The tunica and the extended peripheral zone of the corpus become a " meristematic mantle ". This interpretation is in disagreement with that of Grégoire (1938) in which the reproductive apex is considered to arise as an entirely new structure implanted on the vegetative apex (for reviews of Grégoire's work see Foster, 1939*b*, 1941*a*; Philipson, 1947; Tepfer, 1953). In *Chrysanthemum morifolium* the vegetative apex also shows a gradual transition in zonation pattern at the onset of inflorescence formation (Popham and Chan, 1952). The tunica-corpus organization has been reported to occur not only in the vegetative shoot apex but also in the transition, inflorescence, and floral meristems of *Aquilegia* and *Ranunculus* (Tepfer, 1953) and in *Umbellularia* and *Laurus* (Kasapligil, 1951). The juvenile, adult vegetative and floral apices of *Vinca rosea* also have been described in terms of the tunica-corpus concept (Boke, 1947).

A recent theory of vegetative and floral apical construction, embodying both the tunica-corpus concept and certain of the ideas of Plantefol, has been proposed by Buvat (1951*c*, *d*; 1952). This theory has been reviewed in detail above. It is necessary here only to review briefly the salient features of the theory. In *Myosurus*, *Lupinus* and *Cheiranthus*, Buvat recognizes a central region which includes (*a*) the upper median portion of the tunica (" promériste ème sporogène ") and (*b*) the upper corpus (" promériste ème réceptaculaire "). These two regions constitute the " méristème d'attente " (Fig. 5) which is considered to be inactive during vegetative growth.

The lower or peripheral portion of the two-layered tunica constitutes the " anneau initial " (considered to be the main organogenetic region of the vegetative apex during vegetative growth). Subjacent to the " proméristème réceptaculaire " is a zone in which the cells undergo active transverse divisions characteristic of a rib meristem (" méristème médullaire "), thereby accounting for most of the longitudinal growth of the central axis during the vegetative period of the plant. Only at the time of flowering does the central inactive apical region (" proméristème sporogéne " and " proméristème réceptaculaire ") return to the meristematic state and really become an organogenetic meristem. The " proméristème sporogène ", by renewed activity, forms an extensive layer of initials from which petals, stamens and carpels take their origin. The sepals, however, have their origin from the original " anneau initial " which reportedly disappears at the onset of flowering. This latter assertion agrees with the concept of Plantefol who considers that the sepals are the last appendages to be formed during vegetative functioning of the shoot apex.

Likewise the " proméristème réceptaculaire ", which is inactive during vegetative growth, becomes functional at the onset of flowering and together with derivatives of the activated " proméristème sporogène " gives rise to the entire axis of a flower or inflorescence. Buvat (1952) concludes that there is no ontogenetic continuity between the vegetative stem and peduncle.

The chief objective of Buvat, it would seem, is an attempt to reconcile the Grégoire (*sui generis* interpretation) and Plantefol (transformation interpretation) concepts of the floral apex. This morphological " tour de force " is accomplished by assuming that in vegetative apices of both gymnosperms and dicots, there is a dormant, inactive zone, which, by dedifferentiation, forms the floral apex. This strained effort thus attempts to reconcile (*a*) the numerous demonstrations that the reproductive apices (of both flowers and inflorescences) are transformations of vegetative shoot apices with (*b*) the *sui generis* interpretation of the floral apex.

CYTOHISTOLOGICAL ASPECTS

OCCURRENCE OF ZONATION. Karyological studies of naturally occurring and induced periclinal cytochimeras, together with improved microtechnique methods, have yielded additional informa-

tion on variations in cytological details of the cells of the tunica and corpus (Fig. 6). In several reported instances (Ball, 1941; Boke, 1941; Majumdar, 1942; Hsü, 1944; Philipson, 1947, 1949; Millington and Gunckel, 1950; Gifford, 1950; Rouffa and Gunckel, 1951*a*; Kasapligil, 1951) centrally located corpus initials (Zone 2,

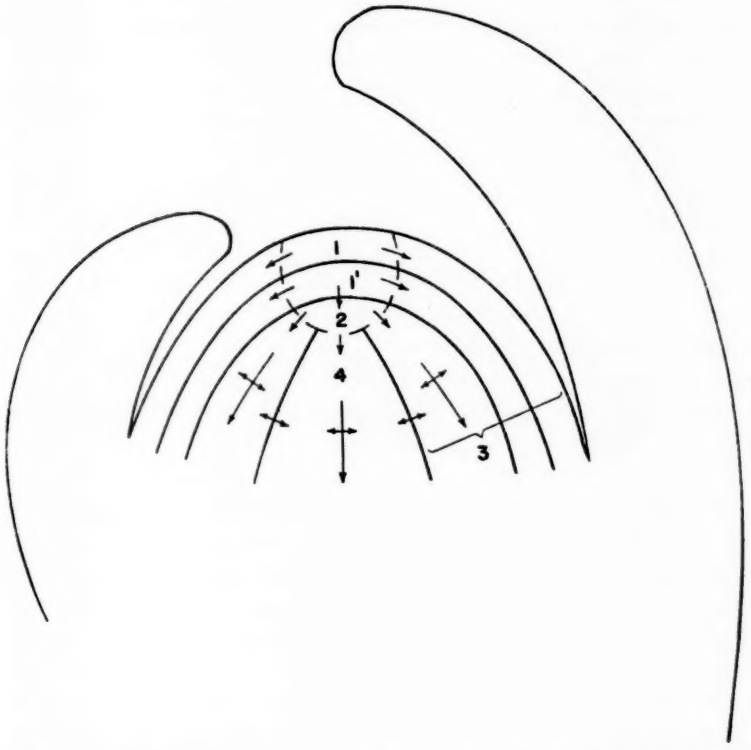

FIG. 6. Diagrammatic representation of growth of the shoot apical meristem of a dicotyledon interpreted in terms of the tunica-corpus concept and cytohistologic zonation. The example is considered to have a two-layered tunica in which occasional periclinal divisions may occur in T_2. *Zone 1, 1'*—initials of tunica layers; *Zone 2*—corpus initials; *Zone 3*—peripheral zone; *Zone 4*—rib meristem. See text for more complete explanation.

Fig. 6) stain lightly in contrast to cells of a lateral peripheral zone (Zone 3) of smaller darkly staining cells. The presence of larger and lighter staining cells may also be characteristic of medianly placed cells of the tunica (Zone 1). The cells of the peripheral zone (Zone 3) are derived in part from the corpus initials and in

part from the tunica initials. These derivative cells divide predominately in the anticlinal plane which results in the presence of several strata of actively dividing cells. This peripheral zone is most conspicuous in relatively large shoot apices. Cells along the lower edge of Zone 2 also contribute cells basally. These derivatives generally exhibit oriented divisions characteristic of a rib meristem (Zone 4) and collectively will become the pith (Fig. 6).

There is an apparent parallelism between the cytohistologically different zones described by earlier workers and those proposed by Buvat (1952). In contrast to Buvat, however, earlier workers (cited above) considered the shoot apex from the standpoint of total activity. The larger and lighter staining cells of the more apical and axial regions (Zones 1, 1′ and 2, Fig. 6) of the shoot apex are considered (or so implied) by these workers to be in a different physiological state than cells in a more peripheral position. Collectively, however, these cells are regarded as the seat of origin of all cells of the primary body even though cells of a subjacent region may be in a more active state as evidenced by their staining qualities (for a more detailed analysis of the problem, see section " MÉRISTÈME D'ATTENTE " CONCEPT).

In addition to the apical zonal patterns described above, Popham and Chan (1950) give considerable importance to a cup-shaped zone of cells in *Chrysanthemum* which lies below the zone of corpus initials and extends up through the peripheral layers (Fig. 7). This zone (Zone 3) is considered as a separate zone interpolated between the mantle and peripheral zones and the zone of corpus initials (central-mother-cell zone of Popham and Chan) and the rib meristem zone. It is during midphase of a plastochron (post leaf initiation and prior to the initiation of the next leaf) that the zone (Zone 3) becomes fully developed. The cells exhibit oriented divisions, and the tissue has the appearance of a cambium as the latter is seen in transverse section. The suggestion is offered by Popham and Chan (1950) that the presence of this zone may be correlated with large apex diameter. Several examples are cited: the apices of *Phoenix canariensis* and *P. dactylifera* (Ball, 1941); *Bellis perennis* (Philipson, 1946); *Opuntia cylindrica*; *Trichocereus spachianus* (Boke, 1941). Vaughan (1952*a*), however, has reported a cambium-like zone in the small apex of *Arabidopsis thaliana*; the apex is 54 microns wide and 23 microns high.

Patterns similar to that displayed by the above genera can be observed in *Drimys Winteri* var. *chilensis* (Gifford, 1950, p. 602, Fig. 13) and *Drimys lanceolata* (Gifford, 1950, p. 604, Fig. 15). In these species the apex is essentially flat with the leaf primordia overarching the apical meristem. Whether the presence of this so-called cambium-like zone (if it should be recognized as a definite

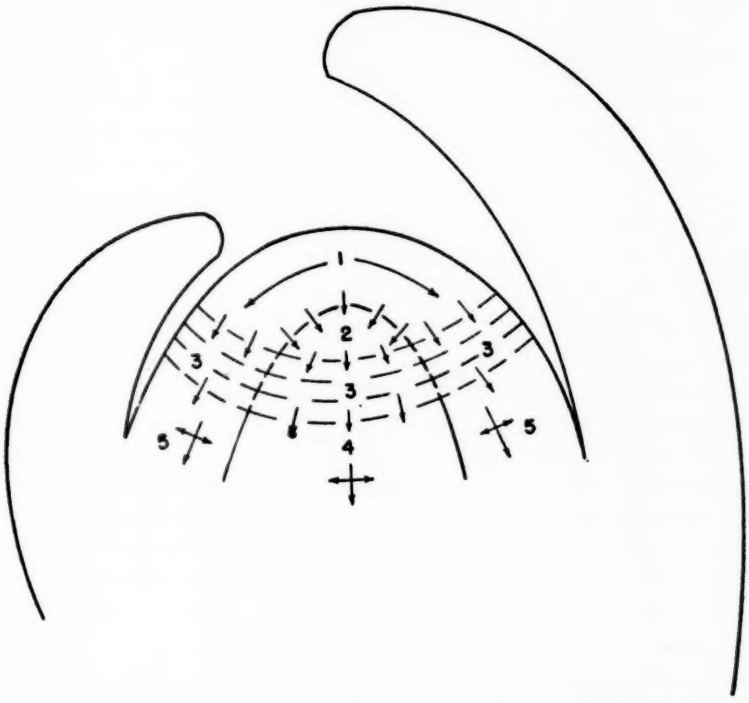

FIG. 7. Diagram depicting organization of a dictoyledonous shoot apex based upon the mantle-core concept. *Zone 1*—mantle layers; *Zone 2*—central-mother-cell zone; *Zone 3*—cambial-like zone; *Zone 4*—rib meristem; *Zone 5*—peripheral zone (after Popham and Chan).

zone) will prove to be correlated with apex size or entirely with plastochron stage, can be determined only by further studies. Possibly the zone in question need not receive special designation because it could be interpreted as an active phase in the growth of the peripheral zone and the rib meristem. In the shoot apex of *Ginkgo,* Foster (1938) considers the presence of a similar zone as simply representing a transition from a region of low mitotic

frequency to one of high activity. As pointed out by Vaughan (1952*a*), it is during a certain phase of a plastochron that this type of pattern should be expected; that is, prior to leaf initiation the shoot apex increases in height (or width) and the type of oriented divisions described would bring this about. The peripheral portion of this zone may correspond to the region of "dedifferentiation" in the sense of Buvat (1950*a*), or to "l'anneau initial" (Plantefol, 1947). In any event this type of growth phase precedes leaf initiation.

DIFFERENTIATION AND DEDIFFERENTIATION. Adopting the tunica-corpus concept, differences in appearance of the chondriome during the ontogeny of the apical meristems of *Cheiranthus cheiri* and *Myosurus minimus* have been studied by Buvat (1950*a*, 1951*b*, 1952). The results of this important study are based upon the killing and fixing of plant material according to the schedule of Regaud, whereby a basic fixation image is achieved. The cells of the shoot apex of a germinating seed in *Cheiranthus* are considered to be meristematic in that they possess abundant cytoplasm, small vacuoles, attenuated chondriosomes and enlarged nucleoli, and are without plastids. After the cotyledons expand, the meristematic cells "differentiate". By this is meant that large vacuoles are formed, the cells have less chromatic cytoplasm, chloroplasts appear throughout the cells, and the nucleoli diminish in size. Correlated with the resumption of growth, there is first a "dedifferentiation" process within cells of the tunica at positions where foliage leaves will appear; this results in a return to the "meristematic" state of that portion of the apical meristem.

The uppermost or more centrally located cells of the tunica and corpus of the seedling apex never "dedifferentiate" entirely or to the extent of those cells which occupy more subterminal and peripheral positions. In fact, in older plants of *Cheiranthus* these differences in the cytoplasmic appearance of cells in various regions of the apex are maintained. The upper cells of the tunica have rather large vacuoles and small nucleoli; those of the upper corpus possess small nucleoli and plastids. The cells of young leaf primordia and those occupying positions of presumptive leaves are considered to be less 'differentiated" in that they have very small vacuoles, finely divided chondriosomes and enlarged nucleoli.

This cytological study by Buvat is particularly commendable be-

cause it represents the first intensive study of cytoplasmic variability of cells within the shoot apical meristem, using special methods. The study corroborates and explains, to some extent, the cytohistological zonation patterns (as revealed by staining reactions) observed in shoot apical meristems when more conventional methods are used (see preceding section, this review). However, extreme caution should be observed in attempting to translate this information into terms of histogenesis for the apical meristem. The cytological appearance of a cell may be simply a reflection of its integrated position within the apical meristem and in no way indicate its actual ontogenetic origin.

VARIABILITY IN SIZE AND STRUCTURE

GROWTH–SIZE CORRELATIONS. Using maize, Abbe and Phinney (1951) have provided us with a valuable contribution toward an understanding of the relation of internal histology to the observed changes in size of a shoot apex during ontogeny. These authors use the term " shoot apex " in a narrow sense—it is that portion distal to the youngest recognizable leaf primordium. They state that " histologically and morphologically, leaf primordia are identifiable at very early stages during their initiation, thereby readily establishing the lower limits of the shoot apex ". The term " plastochron " is used to indicate the time interval between the initiation of successive leaf primordia; " shoot apex stage " is used to indicate that period of the ontogeny which falls within the time limits of the corresponding plastochron. In addition, each shoot apex stage is divided into an early substage (immediately after leaf initiation of the previous plastochron), a mid substage and a late substage (just prior to initiation of the leaf of the present plastochron). The results of these studies revealed that apparently there is a linear relationship between the dimensions of the shoot apex in the successive stages 7–14. The average linear dimensions at any given stage differ from the corresponding average dimensions during the preceding stage and the one next following by an essentially constant amount: 4.8 microns for length, 7.4 microns for width, and 9.0 microns for thickness (in the plane of the leaves). From this information a regular arithmetic increase in length and width of stages 7 through 14 can be determined.

Studies of internal structure (Abbe, Phinney and Baer, 1951)

support the above conclusions. It was found that cell size is approximately constant throughout each stage, and the number of cells therefore follows a pattern of development parallel to that of increase in size of the shoot apex.

PLASTOCHRON VARIATIONS. It is a well-known fact that the vegetative shoot apex exhibits fluctuations in size and form during the production of leaves. These changes can be referred to as "plastochronic variations". The early divisions which mark the site of leaf initiation often cause a lateral protrusion on one side of the apex if the plant has alternate leaf arrangement, or on two sides if the arrangement is distichous or decussate. This protrusion has been termed the "soubassement foliare" (Louis, 1935) or "foliar buttress" (Foster, 1936) or "foliar foundation" (Majumdar, 1942). Continued growth at the site of the buttress results in the formation of the upright part of the leaf primordium. No clear delimitation can be made between the leaf buttress and the upright part of the leaf primordium. At the same time the leaf buttress is not sharply delimited from the shoot apex, an expression of the intrinsic unity of leaf and stem. As a matter of convenience some attempts have been made to distinguish between stages in early leaf initiation and further development, using the terminology of Grégoire (1938). Plantefol (1947) distinguishes an initial ("initium foliare") which reflects nothing more than the presence of preparatory divisions in the future foliar buttress during maximal area phase. The next stage is the development of a definite meristematic protuberance ("primordium foliare") on the surface of the shoot apex. The third stage ("ebauche") is reached when a certain degree of differentiation has taken place, i.e., vacuolation of cells on the adaxial and abaxial sides of the young leaf.

Because of this lack of a clear delimitation between the shoot apex and the emerging leaf primordium, determination of shoot-apex size—width and height—is a real problem. The important question is whether or not the leaf primordium in the stage of leaf buttress should be included in the measurements of both height and width. Workers diverge in their answers to this question. According to Schmidt (1924), during the beginning of leaf initiation the shoot apex attains a maximal area, and after the appearance of a definable upright leaf primordium the shoot apex is reduced to minimal area. Obviously, Schmidt included the leaf

buttress in the determination of size and form of the shoot apex. Whether the foliar buttress is included or not in measurements of width depends somewhat on the form of the shoot apex. In plants which possess essentially flat shoot apices, inclusion of the foliar buttress (or at least that portion of the apex showing the first indication of leaf initiation) is necessary if the measurement of maximum width is to be meaningful.

Other workers exclude the foliar buttress in measurements of width (Popham and Chan, 1950; Rouffa and Gunckel, 1951*a*). Popham and Chan (1950) consider that maximum width is achieved during post initiation stages, specifically during mid-phase of the plastochron in *Chrysanthemum*. Minimum width and diameter are associated with early stages in leaf primordium development. In the reviewer's opinion, the most reliable method of determining maximum width is recognition of the first divisions (generally periclinal) which localize the site of a new primordium. Often these first divisions do not modify the original outline of the shoot apex; therefore, maximum width of the shoot apex is reached at this moment, not before. In this connection, Fig. 2 in the paper by Popham and Chan (1950, p. 478) is cited as being representative of the shoot apex of *Chrysanthemum* at the time of leaf initiation. The shoot apex does not resemble the apex (Popham's Fig. 4) described as being in mid-plastochron, which it should if mid-plastochron phase precedes the stage of leaf initiation.

Most workers are in agreement that the height of the shoot apex should be measured from the level of the youngest definable leaf to the highest point of the shoot apical meristem. Measurements of height may include the foliar buttress or at least the first recognizable initials. If this procedure is not followed, maximum height could never be accurately determined. In a plant with distichous leaf arrangement, the formation of a foliar buttress permits recognition of maximal height of the previous plastochron and minimal height of the present plastochron (see section GROWTH–SIZE CORRELATIONS). Plants with other leaf patterns present problems that are not easily resolved. In order to determine the youngest leaf primordium for measurement purposes, it is most essential that serial longitudinal and serial transverse series of sections be thoroughly studied. The measurements obtained from a study of transverse sections are most reliable.

In the ever increasing volume of literature on the structure and

development of the shoot apex, some attention has been devoted to determining whether topographical and cytological changes occur in the shoot apex during the course of a plastochron. In certain reported instances (Cross and Johnson, 1941; Schnabel, 1941; Reeve, 1942, 1948*a*; Gifford, 1950) a more stratified appearance of the shoot apex (at maximal-area phase of the shoot apex) is reported to be correlated with the initiation of a leaf primordium. Following the initiation or emergence of a primordium in *Salix laevigata* there may be periclinal divisions in cells of the upper layers of the stratified corpus or even in a centrally located cell of the otherwise distinct T_2 layer (Reeve, 1948*a*).

According to Reeve (1948*a*), the occurrence of a periclinal division in T_2 does not make the tunica-corpus concept untenable. It is during this period after emergence of a primordium that periclinal and oblique divisions occur which would establish a new cellular pattern and allow for subsequent enlargement of the shoot apex.

In *Drimys lanceolata* (Gifford, 1950) maximum stratification also is correlated with the initiation of a leaf primordium. Periclinal divisions may occur in central medianly positioned T_2 cells during minimal area phase, and evidence of stratification becomes obscured. Periclinal divisions may occur in the flank-cells of the second tunica layer of *Vinca rosea* (Cross and Johnson, 1941) or even in cells of T_2 toward the tip (Boke, 1947). Rouffa and Gunckel (1951*a*) also reported fluctuations in the tunica of certain members of the Rosaceae but did not consider these changes as being specifically related to periodicity. Millington and Gunckel (1950) also were unable to establish any correlation between the number of tunica layers and plastochron stage in *Liriodendron tulipifera*.

While the preceding discussion concerned the fluctuations or variations in the discreteness of the tunica layers, some workers have interpreted the apparent changes in stratification as an expression of variations in the activity of the corpus. In his intensive work, Schnabel (1941) concluded that, although frequent or occasional periclinal divisions may occur in cells of the tunica, the corpus also exhibits evident layering at times. In an early carefully documented work Zimmermann (1928) followed the ontogeny of the shoot apex in *Hypericum uralum* and concluded that the tunica layers do not fluctuate in a leading shoot but that upper cells

of the corpus form a definite layer at maximal area phase; it is after the emergence of a leaf that periclinal divisions may occur in centrally located cells of this layer. Stratification of corpus initials during maximal-area phase is particularly evident in the shoot apices of *Drimys Winteri* and *D. lanceolata* (Gifford, 1950). Immediately after leaf initiation this alignment is destroyed by the occurrence of periclinal divisions. Cross and Johnson (1941) found that in *Vinca rosea* the upper layer of the corpus may maintain its identity immediately after leaf initiation, but sooner or later the cells divide periclinally so that at least two distinct layers of cells can be recognized in the corpus.

In preceding sections of this review (TOPOGRAPHICAL ASPECTS and CYTOHISTOLOGICAL ASPECTS) the concept of apical structure suggested by Popham and Chan (1950) has been described in considerable detail. From their study of *Chrysanthemum,* Popham and Chan conclude that correlations apparently do not exist " between the number of mantle layers and (1) the volume, height, or diameter of the shoot apexes, (2) presence of a zone of cambial-like cells, (3) the volume of the central mother cell region, (4) stage of development of the leaf primordium, or (5) position of the bud on the stem ". However, they do report that maximum expression of a " cambial-like " zone is associated with a particular growth phase of the shoot apex. In the course of a plastochron, the zone is first apparent in a region (below the central-mother-cell zone) that will eventually become the pith and is correlated with the first indication of leaf initiation. As the newly initiated leaf primordium enlarges, the zone becomes more definite and finally it becomes extended across the mantle to the surface layer. The zone is most conspicuous at midphase of a plastochron. Popham and Chan (1950) suggest that the presence of a cambial-like zone may be correlated with large apex diameter (for a more detailed account see section CYTOHISTOLOGICAL ASPECTS of this paper). In the reviewer's opinion, the time of most rapid growth in height (or width of a flat apical meristem) of a shoot apex corresponds to the mid-phase of a plastochron, and the type of divisions described by Popham and Chan (1950) would account for the observed growth pattern. The zone does not merit special attention except as it is related to changes in growth of the entire shoot apex.

SEASONAL VARIATIONS. Besides the paucity of studies on structure and growth throughout the life of an annual, the possibility of actual seasonal variations in the structure of the shoot apex of perennials remains relatively unexplored. At present, the available information is for the most part contradictory and fragmentary. Millington and Gunckel (1950), in a study of *Liriodendron tulipifera,* concluded that no seasonal changes can be ascribed to the shoot apex. Variations in the number of tunica layers (2 or 3) can be observed in all samples of the shoot apex. They further report that zonation (cytohistological) is less distinct in dormant shoot apices, but they would prefer to interpret this as a response on the part of the plant to physiological changes associated with dormancy and breaking of dormancy. Attainment of maximum width, degree of stratification and expression of cytohistological zonation in two species of *Drimys* are reported to be characteristic of vegetative shoots that have completed elongation for the year. It is during this period that bracts, with their axillary inflorescences, are initiated at the shoot apex.

The researches of Rouffa and Gunckel (1951*a*, *b*) have provided us with the most comprehensive review to date of comparative apical structure in one family. The family Rosaceae was chosen because it includes trees, shrubs and perennial herbs, from which active and perennating buds can be obtained. Rouffa and Gunckel (1951*a*) have concluded that in the Rosaceae, in general, there is no correlation between size and shape of an apex and growth habit, as suggested by other workers (Philipson, 1947; Reeve, 1948*a*), or between height of shoot apex and number of tunica layers. Furthermore, no strict correlations could be established between the presence of cytohistological zonation (presence of a central zone) and growth habit. Some variation in tunica layering was reported to be evident between apices of perennating buds and active shoots, but no generalizations were established. Rouffa and Gunckel (1951*b*) conclude that perhaps it will be more rewarding to seek correlations between the mode of pith development and growth habit rather than to look for correlations within the shoot apex itself and growth habit.

VARIATIONS IN RELATION TO AGE OF THE PLANT. The origin and establishment of functioning apical meristems in the embryo and

their continued development has been described for *Garrya* and *Pisum* (Reeve, 1942, 1948*a, b*). It is reported that in *Pisum* apical "stratification becomes increasingly evident during growth of the embryo". Although stratification may be pronounced in the shoot apex of the adult plant, its structure is the same as in the fully developed embryo. Developmental changes of the shoot apex of *Umbellularia* during different phases of growth have been reported by Kasapligil (1951). The epicotyl apex of a dormant embryo is flat and consists of one tunica layer and an ill-defined corpus-initiating zone. A rib meristem extends very close to the surface. All cells of the apical meristem seem to be densely cytoplasmic. During germination the shoot apex is reported to increase greatly in width and height. However, only a single tunica layer is present. Also, all the cells of the apical meristem take on a hyaline appearance. Cytological zonation becomes apparent through differential vacuolation of certain cells. After germination the size of the shoot apex is again reduced. A well-established T_2 layer, taking its origin from uppermost corpus initials, now becomes evident and is characteristic of the adult shoot apex along with cytohistological zonation. The epicotyl apex of *Laurus* also has a single tunica layer, but a second layer is established when a seedling is three months old.

Increase in size of stem from the time of seed germination to flowering is a common phenomenon in herbaceous plants. Rauh and Reznik (1953) have supplied interpretive histologic descriptions of the changes that occur in the shoot apex during ontogeny which might account for this thickening growth. The study was based upon a selected number of composites and certain representatives of other families.

Tunica and corpus are accepted by Rauh and Reznik as topographical designations not only for the vegetative apex but also for inflorescence and floral apices. The authors rightfully do not consider tunica and corpus as constituting histogens; however, according to the authors, histogens do exist in the shoot apex of certain angiosperms, as evidenced by their cytological zonation patterns. Rauh and Reznik (1953) employ the shoot apex of *Ginkgo biloba,* as described by Foster (1938), as the prototype for the analysis of zonation in the angiosperms used in their study. It is pertinent, therefore, to review at this point the structure of

the shoot apex in *Ginkgo* (Fig. 1). At the tip of the slightly elevated apical meristem is an apical initial group (Zone 1). From the lower edge of the apical group new cells are added to a cup-shaped group of cells referred to collectively as the "central mother cell zone" (Zone 2). By anticlinal divisions of cells along the side of the apical group, derivatives are added to a surface layer, the cells of which may frequently divide periclinally. Ultimately a definite protoderm is developed from this layer. The cells of the central mother cell zone are the largest of the apical meristem. They have less dense cytoplasm than their derivatives and possess large, lightly stained nuclei. Cell enlargement, instead of cell division, seems to be characteristic of this zone. Renewed cell division along the flanks and base of the central-mother-cell zone gives rise to peripheral subsurface layers (Zone 4) and a rib-meristem (Zone 5), the latter being the preliminary phase of pith formation. The surface layer (derived from the apical group) and the peripheral subsurface layers (derived from the central-mother-cell zone) constitute the peripheral zone (Zone 4). The cells of the peripheral zone are uniformly small, stain deeply, exhibit frequent divisions, and give rise to the cortex and procambium, and provide initials for leaf primordia.

Like many other modern students of shoot apices, Rauh and Reznik recognize a cytohistologic zonation which is superimposed over the tunica-corpus pattern. They describe this zonation as follows (Fig. 8). Centrally located cells of the tunica correspond with those of the apical initial group (Zone 1, see above) of gymnosperms and are termed the "central-cell group" (Zentralzellgruppe). The counterpart of the central-mother-cell zone (Zone 2) in gymnosperms is the "pith-mother-cell complex" (Markmutterzellkomplex). A flank or peripheral meristem (Flankenmeristem) is identified with the peripheral zone (Zone 4) of gymnosperms. A pith meristem (Markzellenmeristem), having its origin from the base of the pith-mother-cell complex, gives rise to cells of the future pith.

Although Rauh and Reznik (1953) base their work on generalized zonation patterns in *Ginkgo* and the cycads, they fail to mention that a part of the peripheral zone (Zone 4), as well as the basally situated rib meristem, is derived from the central-mother-cell zone (Zone 2). In descriptions of their material the boundary

between the future pith and the peripheral zone is depicted as being very sharp and easily discernible. Files of cells, derived from the pith-mother-cell complex, are said to end blindly against the peripheral zone, an additional confirmation of the independent origins of the two zones. This concept is not in line with original interpretations of zonation (Foster, 1938). Recognition of a common

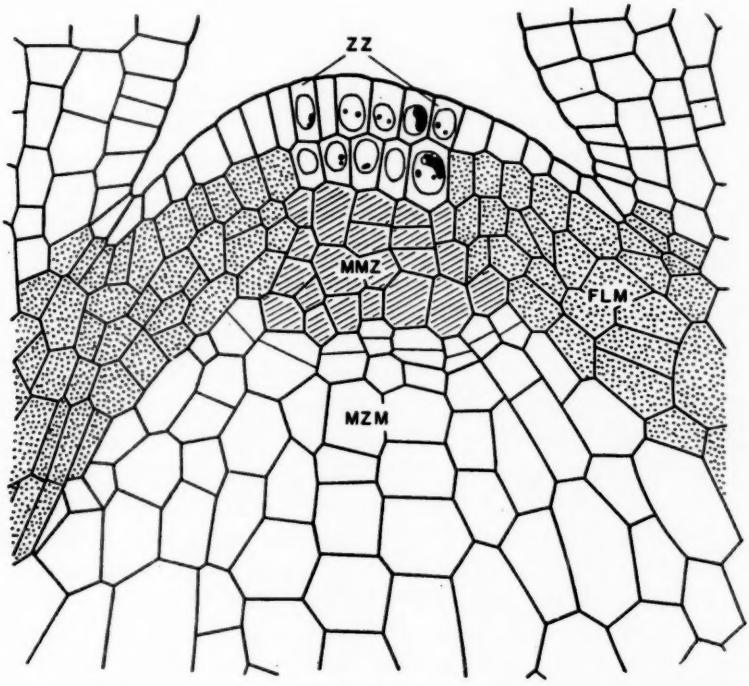

FIG. 8. Diagram, shoot apex of *Zinnia Haageana* based on the histogenetic-zonation concept. *FLM*—"Flankenmeristem" (flank or peripheral meristem); *MMZ*—"Markmutterzellkomplex" (pith mother cells); *MZM*—"Markzellenmeristem" (rib meristem, preliminary phase of pith formation); *ZZ*—"Zentralzellgruppe" (central cells of the tunica) (after Rauh and Reznik).

origin for the pith, procambium and most of the cortex is a fundamental prerequisite for proper understanding of apical organization in most gymnosperms. This recognition is also very important if the concepts of cytohistological zonations are to be extended to the study of shoot apical organization in angiosperms.

The following description of cytological details and development of a dicotyledonous shoot apex, according to the concepts of

Rauh and Reznik (1953), are based on *Jasione perennis* and two species of *Zinnia* (Fig. 8). In *Jasione* the shoot apex of a young plant possesses a two-layered tunica, in which a few centrally located tunica cells can be identified by their large size, weakly staining cytoplasm and clear appearing nuclei. These cells constitute the so-called central cell group. The authors consider this zone to have no special histogenetic significance, although they state that these cells would bring about restitution of the tunica during a plastochron. The number of central cells is said to be correlated with growth in length of the shoot and with an increase in size of the vegetative shoot apex.

The true focal point of growth at the shoot apex, according to Rauh and Reznik, is in the pith-mother-cell complex. These cells have dense cytoplasm, large nuclei which stain relatively weak, and are actively dividing. There may be one initial cell in the seedling apex (*Zinnia Haageana*), but with subsequent growth of the axis a group of initials is established. In addition to cells being added basipetally and toward the flanks of the zone, derivatives may be formed acropetally, an activity which results in a general lowering of the center of activity of the pith-mother-cell complex. No reliable evidence, however, is presented in support of the supposed acropetal addition of cells. Rauh and Reznik (1953) call attention to the cambial-like meristem (pith meristem), said to have its origin from pith-mother-cell complex along its lower edge. As was stated previously in Foster's (1938) original investigation on *Ginkgo,* this particular zone was interpreted as representing simply a transition to rib-meristem activity; this activity is sustained considerably at lower levels. The zone was not considered as constituting a special interpolated cambial-like meristem but merely as a region in which cells exhibit pronounced seriation.

The flank or peripheral meristem (Rauh and Reznik, 1953) which surrounds the developing pith and pith-mother-cell complex consists of cells which are smaller than those of the pith-mother-cell complex and are intensely chromatic. These features also are said to characterize flanking cells in the outer tunica layer. In the vegetative apex the cells of this meristem provide initials for leaf primordia and contribute cells to the procambium and future cortex. The authors give no direct statement concerning the origin of the flank meristem, but apparently consider it as a zone inde-

pendent from surrounding tissues. In studies on angiosperm shoot apices by certain other workers, the peripheral zone is reported to have its origin from upper centrally located corpus initials. The fact that certain cells of the tunica or inner layers of the core (Popham and Chan, 1950) or corpus exhibit the features usually associated with active growth would merely reflect their integrated function by virtue of their position, and in no way would it indicate the origin of the cells. In conclusion it would seem that Rauh and Reznik have introduced a certain degree of artificiality in the distinction made between the pith-mother-cell complex and the flank meristem. A critical analysis of derivative tissues of an apical meristem indicates that it is extremely difficult to draw a definite line between a cell of the peripheral zone or its derivatives and a contiguous cell of the developing pith. This is particularly true when the two cells are obviously derived from a common mother cell.

With continued vegetative growth, the following changes are reported to occur in the activity of the apical meristem and in the relative positions of growth centers (Rauh and Reznik, 1953). There is a change in the form and a continual increase in size of the vegetative shoot apex (independent of plastochronic variations). In some instances there is an increase in the number of tunica layers coupled with a further increase in the number of central cells. There is also a widening and lowering of the pith-mother-cell complex. As mentioned earlier, the first indication of primary thickening growth is related to the widening of the pith-mother-cell complex.

The final expression of zonation is reflected in the organization of the inflorescence apex. The authors state that the tunica-corpus arrangement is present in the inflorescence apex, but this organization has no histogenic value. To the authors, zones are more realistic and constitute histogens. In detail, the pith-mother-cell complex increases further in volume (particularly if a flat receptacle is to be formed), giving rise exclusively to the pith. A uniformly meristematic mantle now covers the pith-mother-cell complex and has had a threefold origin. It is derived (*a*) in part from the stable tunica layers (which no longer have the characteristics of central cells), (*b*) in part from the derivatives of the pith-mother-cell complex formed on its upper edge, and (*c*) in part

from the independent flank meristem. The authors conclude that, topographically, a tunica-corpus organization is present in the inflorescence and floral apex with the unique exception of *Crepis rubra* in which periclinal divisions may occur in the outer tunica layer (the first reported instance for dictoyledons).

In summary, the researches of Rauh and Reznik (1951, 1953) are commendable because they represent the results of extensive life-cycle investigations on the apical meristems of representatives of one family. To follow the development of the shoot apex from the embryo through the vegetative phase to flowering is needed most urgently if an increase in our knowledge of the structure and functioning of apical meristems is to continue satisfactorily. Furthermore, from the work of Rauh and Reznik, it becomes increasingly clear that in addition to the topographical aspects of apical meristem organization, there are evident cytological patterns of fundamental importance. However, the value of Rauh and Reznik's insistence on the histogenetic significance of the zones might be seriously questioned.

EFFECTS OF TREATMENTS OTHER THAN THOSE WITH COLCHICINE. In botanical history there are several reports of experimental wounding of the shoot apices of plants and the recording of the results. Within the last ten years more precise experiments have been performed; not only have the resultant organogenetic products been described, but microscopic examinations have been performed on the altered shoot apices. A considerable volume of this work has been carried out on leptosporangiate ferns by Wardlaw (1949), but the results of this work will not be discussed in the present restricted review.

In the angiosperms, Ball (1950*a*, *b*, 1952) has performed some very exacting surgical operations on *Lupinus albus*. The shoot apex of *L. albus* has a two-layered tunica in which the cells of the inner layer may divide periclinally. After removal of a wedge-shaped piece of tissue from the shoot apex, cells on the flanks of the original shoot apex which would normally produce foliar primordia often give rise to new shoot apices. Periclinal divisions in cells of the second tunica layer contribute derivatives to the new corpus. After the new apices have been established, they resemble those of the untreated plant in every detail. From the

observed results, Ball questions the individuality or complete distinction of tunica and corpus, and demonstrates that derivatives of centrally located tunica and corpus cells are morphogenetically equivalent to the original medianly positioned initials (Ball, 1950*b*).

The report of Buvat (1950*c*) has provided us with an initial insight into the cytological variation of the vegetative apical meristems of plants grown under different environmental conditions. In the apices of *Lupinus albus,* grown in the greenhouse during the months of January to March, under conditions of relatively high temperature and medium light, plastids could be identified in cells of both the tunica and corpus. In another series of plants of the same species, grown outside during April and May under strong light conditions and relatively low temperatures, the cells of the tunica were uniformly meristematic; plastids were indistinct or very little differentiated, while chloroplasts were formed in the corpus. Buvat (1950*c*) concludes from these studies that the causes of these observed fluctuations are probably of internal origin but that they are influenced by external conditions. A comparison of similar organogenetic stages would be of utmost importance in studies of this type.

Profound morphogenetic changes may occur in the shoots of plants treated with 2,4-D or other growth-regulating substances. The results of one study (Gifford, 1953) indicate that the shoot apical meristem of cotton plants treated with sublethal dosages of 2,4-D are not morphologically altered. The effects of 2,4-D on development become apparent only some time after leaf primordia are initiated. However, a critical cytological study has not been performed on the shoot apices of treated plants.

TYPOLOGY

Long before the renaissance of interest in shoot apical meristems of angiosperms, considerable effort was directed toward the establishment of root apical meristem types based upon descriptive accounts. Type "numbers" were assigned each new type encountered, and this was done not by one individual but by several investigators. Subsequent workers labored to categorize their specific research entity or announce a new type. The study of root apical meristems became a formalized endeavor, losing much of its appeal as an enquiry into the origin of patterns in the root and

subsequent growth and differentiation of derivative cells and tissues.

At present the descriptive study of shoot apical meristems is in the same danger of becoming over-formalized. Recently (Popham, 1951) the apices of vascular plants have received the treatment originally unique in the study of root apical meristems. Popham (1951) has proposed seven numbered types. The first type is characterized by apices which exhibit a discrete apical cell. Apical growth by two to five apical cells is a second pattern which is featured in " transitional " lower vascular plants. Three other types are established for lower vascular plants and gymnosperms.

In the angiosperms a distinction is made between those apices (the *Opuntia* type) reported to have a cup-shaped cambial-like zone which is interpolated between the initiating zones and subjacent meristematic tissues, and those lacking such a zone. Popham and Chan (1950) suggest that the presence of a " cambial-like " zone may be related to large apex diameter because it is observable in forms like *Chrysanthemum, Bellis, Opuntia* and *Trichocereus.* Later (Popham, 1951) *Liriodendron tulipifera* was included in this type, although the average apex-width measures only 180 microns. Vaughan (1952*a*) reported a similar zone to be present in the small shoot apex of *Arabidopsis thaliana.*

Popham (1951) points out that whether each plant is correctly typed depends on the accuracy and thoroughness of the observations. Indeed, these requisites are most essential in studies of the shoot apical meristem. Strict adherence to these principles in intensive studies of plastochron and seasonal changes might yield two or more characteristic types for each plant. While it is the intent on the part of Popham to summarize and to classify the growth patterns of apical organization, these patterns have received generic or plant-group designations which may in the future lead to considerable confusion. For example, a dicotyledonous shoot may at one time exhibit the " usual angiosperm type " and at another time, the " *Opuntia* type ". Simultaneously, over the entire plant, the " usual angiosperm type " might be coexistent with the " *Opuntia* type ", depending upon the particular developmental phase of any given shoot. Would not a simply descriptive account be sufficient and preferable, interpreted in terms of the formative activities of an apex at any particular moment?

If establishment of nominal types is necessary, it would seem ap-

propriate to recognize three distinct types of shoot apices that possess single apical cells: (*a*) those with an apical cell having two convex sides, (*b*) those with a biconvex or three-sided pyramidal apical cell, and (*c*) those with a tetrahedral pyramidal apical cell. In the evolution of single characters, specialization in the form of the apical cell may be just as important as recognizing a type which exhibits two to five apical cells. Furthermore, whether there is a single apical cell or a group of apical cells, subjacent tissues are initiated in approximately the same manner in the two types.

PHYLOGENY

In the many papers on the vegetative shoot apex in angiosperms, considerable space is devoted to discussions pertaining to similarities and differences between apices of various genera and species. A review of the literature on apical meristems yielded information which is considered to be of interest not only to the anatomist but also to investigators seeking a plant with certain prerequisite characteristics for their particular research.

To the writer's knowledge there is only one recent tabulation of the results of investigations on the shoot apex in angiosperms (Popham, 1951). A list of the entries included in the latter paper and the results of additional and more recent studies are included in Table I. Information, in a very limited way, is available in about 64 families, 145 genera and 172 species. Reference is made only to the size of the apex and the number of tunica layers present. The data on the dimensions of the apex should be taken with some reservation, since the methods of delimiting the apex are not uniform in the different researches. Moreover, the size is recorded only when it is given by the original author. Whether a "flexible use" (Millington and Gunckel, 1950) is made of the tunica-corpus concept or whether this concept is replaced by that of mantle and core (Popham and Chan, 1950), the data are in agreement in that they emphasize the variability in the degree of stratification or layering of cells in the shoot apices of angiosperms. In Table I the entries with an asterisk represent the number of tunica layers generally present. Only studies dating from the original work of Schmidt (1924) have been recorded, since it is difficult to interpret earlier works in the light of the tunica-corpus concept.

Close examination of the tabulated results reveals no strict cor-

relation between the number of tunica layers, size of apex, and any selected number of morphological features which might be used for correlation purposes. A very obvious fact is the extremely small percentage of investigated forms as compared with the total number, for example, of dicotyledonous species. Unfortunately very few survey studies have been attempted in a single family or a series of related families. To the writer's knowledge only three such studies have been made in recent times, one dealing with several representatives of the Amentiferae (Reeve, 1948*a*) and the others with the family Rosaceae (Rouffa and Gunckel, 1951*a*) and certain members of the Ranales (Gifford, 1950). In certain genera of the families included in the Amentiferae (*Salix, Carya, Quercus, Castanopsis, Lithocarpus, Myrica, Garrya, Morus*) the apex uniformly possesses two tunica layers as the norm. Where variation exists it can be related to periodicity of the shoot apex in the production of appendages. Several genera in the Ranales likewise possess two tunica layers with some seasonal variation as well as fluctuations associated with the course of a plastochron (Gifford, 1950).

Rouffa and Gunckel (1951*a*) have made an extensive survey in the Rosaceae of apical structure in 54 species divided between four subfamilies. The tunica-corpus concept was adopted by the authors and found adequate for descriptive purposes. In summary, their results indicated that no correlation exists between size of apex and number of tunica layers. The number of tunica layers did not seem to be of specific taxonomic significance, although they did speculate upon the possible trends within the family. Most of the members of the subfamily Spiraeoideae, considered primitive in the family, possess a two-layered tunica. The subfamily Rosoideae, although a heterogeneous group, has two or three tunica layers in the majority of cases. Examples of apices with several tunica layers occur in the subfamilies Prunoideae and Pomoideae, considered to be more advanced as regards floral structure. A tabulation of the results of this study has not been included in Table I because the original data are presented in a clear and concise manner and can be consulted for details.

Examination of the dicotyledons reveals the occurrence of one tunica layer in several instances (*Scrophularia, Opuntia, Trichocereus, Echinocereus, Coryphantha, Sambucus, Valeriana*), whereas

a highly stratified condition (four or five tunica layers) is reported in the families Nepenthaceae, Guttiferae, Rosaceae, Hippuridaceae, Caprifoliaceae and Compositae. Approximately 64% of all investigated dicotyledons possess a two-layered tunica.

It is known that a single tunica layer is present in many monocotyledons. This feature, correlated with the active participation of the outer layer in leaf development, and occasional periclinal divisions in this layer at the extreme shoot tip (maize, Sharman, 1940; *Agropyron,* Sharman, 1943; *Chlorogalum,* Sterling, 1944; *Saccharum,* Thielke, 1951) invites comparison with gymnospermous shoot apices. In this connection, *Saccharum* (Thielke, 1951) is particularly interesting. It is reported that the vegetative apical meristem is normally devoid of a stable outer layer, and it is described as possessing a " naked corpus ".

Periclinal divisions have not been observed in the outermost tunica layer of vegetative shoot apices of dicotyledons investigated thus far. Furthermore, in early leaf initiation in dicotyledons the second and third layers participate actively and the outer layer remains as a discrete entity. However, the latter type of development apparently occurs only rarely in the monocotyledonous genera (*Tulipa,* Sass, 1944). A three-layered tunica is reported in the genus *Vanilla* (Orchidaceae) and a four-layered tunica in *Narcissus* (Amaryllidaceae).

The degree of apical layering, as indicative of advancement, interested earlier workers in this field of enquiry. Douliot (1890, 1891) investigated a number of dicotyledonous families and concluded that a trend exists from less stratification in the apetalous forms to increased layering in the Dialypetalae (apopetalous) and Gamopetalae (sympetalous). In the Dialypetalae increased stratification was correlated with the occurrence of an inferior ovary. Interpretation of material was based upon the " histogen theory " of apical structure. Selected examples from Table I agree with the above thesis, but exceptions exist.

The evidence of apical construction has been used again recently for evaluating the primitiveness of families. In the study of several representative apocarpous dicotyledons, Ozenda (1949) compared the apices of genera in the following families: Magnoliaceae—*Liriodendron* and *Magnolia* (four species); Anonaceae—*Asima triloba* and *Anona cherimalia*; Dilleniaceae—*Dillenia in-*

dica; Illiciaceae—*Illicium*. In this group of plants apices are more or less similar in shape, being convex except in the family Anonaceae. In the latter family the apex is more conical in form. Ozenda discusses the possibility that stratification may be indicative of advancement but concludes from his studies that no proof exists of less stratification in these primitive families. He reports that the average number of tunica layers fluctuates from four to five, with six or seven layers characteristic of the Illiciaceae. These observations, in the cases of *Liriodendron* and *Illicium*, are not in agreement with similar studies by other investigators on these two genera. Millington and Gunckel (1950) reported a two-layered tunica, with some variation, in *Liriodendron*; *Illicium* was also reported to have a two-layered tunica (Gifford, 1950).

Several systems of angiosperm classification have been proposed and claims made that each represents a natural system. In addition to this type of approach, other workers have suggested that relative advancement of a family can be worked out on a correlative basis. One such attempt has been made by Sporne (1949). This worker made a statistical analysis of certain floral and vegetative characters possessed by the families of modern dicotyledons and fossil dicotyledons, and found apparent correlations among primitive characters on the one hand, and among the advanced on the other. In addition, these two groups of characters are intercorrelated, but it is possible to distinguish the primitive from the advanced. Each family is then assigned an advancement index expressed in percentages. It is interesting to note that the family Hippuridaceae has an index of 95%. The family Scrophulariaceae has a rating of 92%, but a representative of the family (*Scrophularia*) has a relatively unstratified shoot apex. In *Hypericum* (Guttiferae) there is a tunica of four layers, and the family has an advancement index of only 33%. Thus it would appear that no strict correlation exists, according to this system, between layering and degree of phylogenetic advancement. The results of the study by Sporne (1949) suggest that the ancestral dicotyledon was a tree or shrub with alternate, glandular, stipulate leaves. Flowers were numerous, actinomorphic and polypetalous, with many stamens and numerous carpels. In addition the flower is reported to have been "unisexual".

Although the apical meristem should be studied in many more

families with thoroughness before the possible trends in apical structure can be visualized, it is permissible to speculate as to how the angiospermous apical structure could arise and be perpetuated. It is quite possible that here we are dealing with " differences not adaptive of themselves but developmentally correlated with adaptive characters " (Stebbins, 1950). For example, if, by mutation, a leaf is produced which has strong positive adaptive features and is favorably acted upon by natural selection, the structure of the apex, whether it be the original condition or structurally altered, would become part of the new morphological features of the plant. Such a process might well account for slight but apparent differences in anatomical structures between species of a genus.

During the Cretaceous, when differentiation of angiosperm families was progressing at a rapid rate, the correlation between adaptive features and non-adaptive characters (in themselves) could have been easily realized. Once a particular mode of apical structure was established, it could characterize the entire potential of the family or be modified along with generic specialization.

Also it is quite possible that there has been random association of unrelated and non-correlated features in the evolution of the shoot apex. A gene mutation affecting apical construction would not necessarily have to affect final leaf form. This mutation could be " fixed " through association with the product of some other unrelated ontogeny (floral) which was favorably acted upon by natural selection.

It is quite apparent that the study of the shoot apex should be extended to include many more families, particularly a representative number of genera and closely related species within each family. There is a great need for a much more broadened outlook on the shoot apex of monocotyledons. Most of our generalizations for this group have been based too strongly on the grasses. These extensive and intensive studies may reveal phylogenetic trends in apical structure within the angiosperms.

CONCLUSIONS

Functionally, the shoot apical meristem can be considered as the continuation of embryogeny. The meristem may continually initiate the axial component of the primary body and give rise to appendages of the shoot throughout the life of a plant or it may

enter a state of periodic quiescence. In some plants the vegetative shoot apex may terminate in an inflorescence or initiate lateral inflorescence and floral rudiments.

Recent investigations have corroborated earlier reports that basically the shoot apex of angiosperms can be described in terms of planes of cell division. The shoot apex consists of a peripheral layer or layers of cells that are engaged primarily in surface growth by anticlinal divisions and enclose a group of cells that divide in various planes. The two zones are interdependent growth zones and vary in their contributions to the primary plant body. The supposition that apical initials may exist in an organized meristem has been strengthened through important studies of induced cytochimeras. In function and position, a group of apical initials may exist only temporarily, and adjacent cells may usurp their function through cellular displacements and rearrangements or in response to experimental treatments. The initiation of primordia and growth of the axis cannot be divorced from the activity of centrally located initials of the apical meristem. Attempts to minimize the importance of an apical group are unrealistic in approach.

Superimposed upon the two growth zones of contrasting planes of cell division there is frequently a cytohistological zonation pattern which undoubtedly reflects the integrated functions of cells by virtue of their position. However, the cytologic specialization of a cell in the apical meristem may not be indicative of its origin, and extreme caution must be exercised in establishing cellular lineages.

Even from the limited studies available, it is reasonable to assume that the shoot apex of most seed plants probably exhibits both structural and cytological variations from germination of the embryo to the functioning of the "adult" plant. However, whether changes in stratification and cytohistologic zonation will prove to be correlated with plastochronic changes is for the present undecided. Only limited and contradictory reports are available. We do know that in the time interval between the initiation of one leaf and that of the next there is a period of active shoot-apex growth. During this interim the site of active cell division may not be in uppermost initials but in derivative cells distal to the tip. On the flanks of the apical meristem, these cells occupy the position of presumptive leaves, and they may have more embryonic cytologic features than more terminally disposed cells. Because of these

cellular differences, certain workers would consider that the shoot apex itself exhibits the processes of "differentiation" and "de-differentiation". If this proposal is adopted, the usefulness and practicability of these terms are in danger of becoming overextended.

Whether there are definite seasonal fluctuations in stratification and cytologic zonation of the shoot apex of a perennial plant is virtually an unexplored field; the present conflicting results, however compelling for each investigated species, are based upon only a few plants, and no general conclusions can be established.

In recent years the various theories of interpretation of the flower have been tested by histogenetic investigations. From these studies emerges a well-documented contention that inflorescence and floral mristems exhibit essentially the same structure as the vegetative shoot and that they can be interpreted as derivative forms.

One scheme of classifying or typing shoot apical meristems in all vascular plants has been proposed. While the establishment of systems of classification may represent one of man's most interesting preoccupations, he is, in so doing, enforcing a certain degree of rigidity upon living dynamic systems. Herein lies the danger of imposing formalization and oversimplification upon a complex integrated continuum of life.

No clear phylogenetic scheme in angiosperms, based upon shoot apex structure, emerges from a compilation of investigative results. Indications are strong in a few specialized genera and in some restricted groups that evolution is progressing toward increased stratification at the shoot apex.

The shoot apex of angiosperms has received much attention in recent years, but extensive surveys of entire families should be undertaken. From these studies our knowledge and hopefully our understanding of ontogeny will be extended. In addition, valuable information will be available which may assume importance in the final solution of angiosperm phylogeny.

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TABLE I

DICOTYLEDONS

Families and genera	Size of shoot apex in microns[1]	Number of tunica layers	Investigator
Winteraceae			
Drimys (2 spp.)	98–130 wide, active shoot; 130–164 wide, dormant shoot	2*	Gifford (1950)
Pseudowintera	147–164/32	2	"
Schisandraceae			
Kadsura	262/62	2	"
Illiciaceae			
Illicium	221 wide	2	"
Trochodendraceae			
Trochodendron	229–240/65	2*	"
Tetracentraceae			
Tetracentron		2*	"
Magnoliaceae			
Liriodendron	140 wide; 180 wide[4]	2*	Millington & Gunckel (1950)
Lauraceae			
Laurus	141–168/38–50	2*	Kasapligil (1951)
Umbellularia	147–222/51–90	2*	"
Cinnamomum	128–180/30	2	"
Persea	160–270/22–57	2	"
Notaphoebe	230–246/75–86	3	"
Sassafras	175–195/20–25	2	"
Ranunculaceae			
Myosurus		2	Buvat (1951*a*)
Clematis	132–218/45–160[3]	2*	Schnabel (1941)
Aquilegia		2*	Tepfer (1953)
Ranunculus		2*	"
Calycanthaceae			
Calycanthus		2	Rauh & Reznik (1951)
Moraceae			
Morus		2	Cross (1936)
Ficus carica		1	Rauh & Reznik (1951)
Ficus religiosa		2	Mitra (1950*c*)
Nepenthaceae			
Nepenthes		4	Kühl (1933)
Tropaeolaceae			
Tropaeolum	140/55	3*	Ball (1944, 1948)
Linaceae			
Linum		1*	Esau (1942)
Guttiferae			
Hypericum	170/80	4	Zimmerman (1928)
Violaceae			
Viola		2*	Arnal (1945)

TABLE I (*Continued*)

Families and genera	Size of shoot apex in microns [1]	Number of tunica layers	Investigator
Cruciferae			
Descurainia		2	Dittmer and Spensley (1947)
Brassica		2 [6]	Chakravarti (1953)
Papaveraceae			
Papaver		4 *	Bersillon (1951)
Caryophyllaceae			
Dianthus caryophyllus		2	Shushan & Johnson (1949)
"		2 *	Schnabel 1941)
Silene		3 *	"
Honckenya	125–175/56–185 [3]	2 *	"
Salicaceae			
Salix		2 *	Reeve (1948*a*)
Polygonaceae			
Polygonum		3 *	Mitra (1945)
Ericaceae			
Rhododendron		2	Foster (1937)
Vaccinium		2 *	Dermen (1947)
Oleaceae			
Syringa	218/36	2	Schmidt (1924)
Syringa		1 *	Vaughan (1952*b*)
Ligustrum ibota		2	Schmidt (1924)
Ligustrum vulgare		2 *	Schwarz (1927)
Forsythia		2	Schmidt (1924)
Gentianaceae			
Frasera		2	McCoy (1940)
Centaurium		2	Halmai (1935)
Apocynaceae			
Vinca rosea	160/50	2	Cross & Johnson (1941)
Vinca rosea		2 *	Boke (1947)
Vinca minor	139/42	3	Schmidt (1924)
Ervatamia		2	Mitra (1950*a*)
Polemoniaceae			
Phlox		2 *	Miller & Wetmore (1946)
Solanaceae			
Datura		2	Satina et al. (1940)
Lycoperiscon esculentum	100–160/40–80	2	Steinberg (1950)
Solanum sodomaeum	90–180/30–90	2	"
Solnum tuberosum	135–200/35–85	2	"
Solanum nigrum	100–180/45–175	3 *	"
Scrophulariaceae			
Scrophularia	222/102	1	Schmidt (1924)
Veronica speciosa	285/80	3	"
Veronica myrtifolia	253/102	2	"

TABLE I (*Continued*)

Families and genera	Size of shoot apex in microns [1]	Number of tunica layers	Investigator
Acanthaceae			
Dianthera	160/45	2*	Sterling (1949)
Labiatae			
Plectranthus		2*	Schwarz (1927)
Rosaceae			
Rubus (3 spp.)	50/100	3*	Engard (1944)
Rubus (1 sp.)	50/100	2	"
Amygdalus		4	Brooks (1940)
Mespilus		2	Schmidt (1924)
Crataegus		2	"
"Apple" (6 vars.)		2*	Blaser & Einset (1948)
Northern Spy apple		2	Einset, Blaser & Imhofe (1946)
Rosa centifolia	90–100/80–100	3	Mitra (1949)
Rosa		1	Rauh & Reznik (1951)
Geum		2	"
Leguminosae			
Cytisus		2	Schmidt (1924)
Laburnum		2	"
Acacia	125–130 wide	3*	Boke (1940)
Lupinus	250/81	2*	Ball (1948, 1949)
Glycine	80–120/30–50	2	Sun (1950)
Pisum		3[6]	Reeve (1948*b*)
Pisum sativum		2	Mitra (1950*b*)
Hydrangaceae			
Deutzia		3	Schmidt (1924)
Crassulaceae			
Sedum	100 wide	2	Astruc (1949)
Melastomaceae			
Heterotrichum		3	Weidt (1935)
Hippuridaceae			
Hippuris		5	Louis (1935)
Cactaceae			
Opuntia	400–800 wide	1	Boke (1941)
Trichocereus	700–900 wide	1	"
Echinocereus	600–750 wide	1	Boke (1951)
Coryphantha	600–750 wide	1	Boke (1952)
Echinopsis		Many layers	Wardlaw (1952)
Mammillaria	1200–1500 wide	1	Boke (1953)
Myrtaceae			
Melaleuca		2	Schmidt (1924)
Elaeagnaceae			
Elaeagnus		2	"
Juglandaceae			
Carya		2	Foster (1935)
Fagaceae			
Quercus		2	Reeve (1948*a*)

TABLE I (*Continued*)

Families and genera	Size of shoot apex in microns [1]	Number of tunica layers	Investigator
Fagaceae (*Cont'd*)			
Castanopsis		2	Reeve (1948*a*)
Lithocarpus		2	"
Myricaceae			
Myrica		2	Reeve (1948*a*)
Garryaceae			
Garrya	120–180 wide	1*	Reeve (1942)
Cornaceae			
Cornus (3 spp.)		2	Reeve (1948*a*)
Umbelliferae			
Heracleum	170/80	3	Majumdar (1942)
Caprifoliaceae			
Viburnum rufidulum	225/100	4	Cross (1937)
Viburnum opulus		2	Cross (1938)
Sambucus racemosa		1	Schmidt (1924)
Sambucus nigra		1	"
Sambucus nigra		2	Philipson (1947)
Lonicera japonica		2	Schmidt (1924)
Lonicera iberica		2	"
Valerianaceae			
Valeriana		1	Philipson (1947)
Campanulaceae			
Jasione		2	Rauh & Reznik (1953)
Dipsacaceae			
Dipsacus		2	Philipson (1947)
Succisa		2	"
Knautia		2*	Rauh & Reznik (1953)
Compositae			
Centaurea		1	Rauh & Reznik (1953)
Helianthus annuus		2*	"
Crepis		1	"
Rudbeckia		2*	"
Zinnia elegans		2*	"
Zinnia Haageana		2*	"
Tagetes		2*	"
Echinops		2	"
Artemisia		3	Diettert (1938)
Chrysanthemum morifolium			
var. *Bittersweet*	200–325/40–130	2*	Popham & Chan (1950)
" *Orchid Queen*		4*	"
Chrysanthemum leucanthemum		2	Lawalrée (1948)
carinatum		2	Rauh & Reznik (1953)
Galinsoga		2	Lawalrée (1948)
Bidens		2*	Graf (1937–38)

TABLE I (*Continued*)

MONOCOTYLEDONS

Families and genera	Size of shoot apex in microns [1]	Number of tunica layers	Investigator
Typhaceae			
Typha		1	Schalscha-Ehrenfeld (1940)
Potamogetonaceae			
Potamogeton		2	"
Ruppia		1	Pottier (1934)
Cymodocea		2*	"
Posidonia		2*	"
Pontederiaceae			
Heteranthera		1	Schalscha-Ehrenfeld (1940)
Bromeliaceae			
Ananas		1	Krauss (1948)
Gramineae			
Avena	112/96	1	Kliem (1937)
Triticum	175/120	1	Rösler (1928)
Agropyron		2	Sharman (1943)
Zea mays	89/127	1	Abbe et al. (1941)
Zea mays	119–144/88–162	1	Abbe et al. (1951)
Zea mays		1	Bonnett (1953)
Sinocalamus	30–140/50–120	2*	Hsü (1944)
Dactylis sp.		1	Bugnon (1924)
Dactylis glomerata		2	Thielke (1951)
Molinia		2	"
Melica		1	Bugnon (1924)
Phyllostachys		2[5]	Porterfield (1929–30)
Phragmites		2	Thielke (1951)
Glyceria		2	"
Zizania		2	"
Bambusa		2	"
Phalaris		2	"
Oryza		2	"
Oplismenus		1	"
Panicum		1	"
Sorghum		1	"
Saccharum		No stable tunica	"
Commelinaceae			
Tradescantia			
albiflora	105/120[3]	2	Rüdiger (1939)
virginica	242/197[3]	2	"
Hydrocharitaceae			
Stratiotes		2	Eckhardt (1941)
Cyperaceae			
Carex		1	Stant (1952)
Iridaceae			
Iris		2	Rüdiger (1939)

TABLE I (*Continued*)

Families and genera	Size of shoot apex in microns [1]	Number of tunica layers	Investigator
Palmaceae			
Phoenix canariensis	187/528	1	Ball (1941)
Phoenix dactylifera	187/528	1	"
Washingtonia filifera	175/288	2	"
Trachycarpus excelsa	175/288	2	"
Juncaceae			
Luzula		2 *	Stant (1952)
Amaryllidaceae			
Narcissus		4 *	"
Allium porrum		1	Rüdiger (1939)
Allium cepa		1	Eckhardt (1941)
Liliaceae			
Tulipa	125/375	1	Sass (1944)
Endymion		1 [5]	Chouard (1937)
Aloe	112/130 [2]	2	Rüdiger (1939)
Convallaria		1	Stant (1952)
Liriope		2	Eckhardt (1941)
Mondo		1	"
Orchidaceae			
Vanilla	150/140 [2]	3	Rüdiger (1939)

* Denotes cases in which there appears to be a fluctuation in the number of tunica layers. The figure represents the number of tunica layers generally present.

[1] Where measurements are available from original papers, they are presented by indicating the width first, followed by the height unless otherwise indicated. Measurements are in microns. Measurements made at level of first visible primordium.

[2] Measurements made at level of second visible primordium.

[3] Measurements based on a " double plastochron ".

[4] Larger measurement coincides with a line drawn through base of the petiole; smaller measurement made at stipular axils.

[5] The present reviewer's interpretation in the absence of a direct statement in the original work.

[6] Embryo or young seedling generally has one less layer in the tunica.

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Future Contents of

THE BOTANICAL REVIEW

Articles Received and Awaiting Publication

Wood Fiber Length as Related to Position in Tree and Growth	Stephen H. Spurr *University of Minnesota*
Compression Wood in Conifers as a Morphogenetic Phenomenon	
Seed Germination Problems in the Umbelliferae	Richard Robinson *University of California*
Some Historical Chapters on Tree Growth	R. A. Studhalter *Texas Technological College*
Growth Rings and Climate	Waldo S. Glock *Macalester College*
Apomixis in the Angiosperms. II.	Axel Nygren *Agricultural College of Sweden*
Correlations of ontogenesis in higher plants	A. Takhtajan *Molotov State Univ. of Erevan*
Disinfection of soil by heat, fumigation, and flooding	A. G. Newhall *University of California*
Studies of mineral nutrition by the use of tracers	Orlin Biddulph *State College of Washington*
Fine structure in degraded, ancient and buried wood, and other fossilized plant derivatives	J. Sen *Calcutta University*
Fungi That Attack Microscopic Animals	C. L. Duddington *The Polytechnic, London*
The Phytogeography of Unglaciated Eastern United States and Its Interpretation	E. Lucy Braun *Cincinnati, Ohio*
Genetics and Selective Breeding of Sugar Beets in the USSR	Alexander Archimowitsch *Agricultural Institutes in USSR*
Control of Plant Diseases by the Use of Antibiotic Organisms	R. K. S. Wood and M. Tveit *Imperial College, London*
The Vegetation of Alberta	E. H. Moss *University of Alberta*